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Abstract

Fighting involves the repeated performance of demanding agonistic behaviours and winners usually fight more vigorously than losers. While *vigour* describes the rate and duration of a behaviour, *skill* refers to well-coordinated motor movements. We investigate the role of skill in animal contests for the first time, focussing on the shell-rapping behaviour of hermit crabs during contests over the ownership of gastropod shells. We quantified vigour by recording the total number of raps and the mean number of raps per bout, and we quantified skill by measuring the distances that attackers displaced their shell during each rap. Winners displaced their shells through shorter distances compared to losers, indicating that motor pattern, as well as vigour, differs between contest outcomes. Both vigour and skill improved as fights progressed for eventual winners, but worsened for losers. We suggest that in a contest, skilful motor movements allow vigorous fighting, and both aspects deteriorate with fatigue. Skill may be important in the wide range of contests where outcomes are driven by energetic constraints. Understanding the links between skill, vigour and energy could provide new insights into strategic decision-making during animal contests.

Key words: Contest, fight, skill, vigour, RHP, decision-making

Introduction

A key determinant of victory in a contest is the difference in fighting ability, or resource holding potential (RHP) between opponents (Humphries et al., 2006) and the importance of RHP variation has been clearly demonstrated among arthropods in particular (Vieira & Peixoto, 2013). Therefore, efforts have been made to uncover the traits that might influence RHP. Intuitively, larger individuals should be better at fighting and overall body size is commonly used as a proxy for RHP (Briffa, Hardy, Gammell, Jennings, Clarke & Goubault, 2013). In contests where weapons are used, for example, larger individuals should have larger and potentially more powerful weapons (Sneddon, Huntingford & Taylor, 1997). Even in non-injurious contests weapons may be used in static displays (e.g. Huntingford, Taylor, Smith & Thorpe, 1995; Sneddon et al. 1997) or dynamic displays (e.g. Bridge, Elwood & Dick, 2000; Morrell, Backwell & Metcalfe, 2005) that advertise RHP through costly repetition (Payne and Pagel 1997; Payne 1998). The rate and duration of repetitive displays is usually described as the *vigour* of the display (Briffa & Elwood 2004; Byers, Hebets & Podos 2010). In contests, winners tend to display more vigorously than losers, and in some cases winners escalate in vigour as the fight progresses (Briffa, Elwood & Dick, 1998; Briffa & Elwood, 2000a; Jennings, Gammell, Payne & Hayden, 2005). In addition to variation in the ability to perform vigorously, fighting animals might vary in their ability to perform these movements in a coordinated and precise way, an attribute described as *skill*. Thus, *vigour* is the ability to perform energetically expensive motor acts repeatedly whilst *skill* is defined as the ability to perform these challenging actions ‘well’ (Byers et al. 2010). A challenging action is one that requires precise activation and coordination of motor units, exceeding the requirements of routine activities (Byers et al. 2010; Manica et al. 2016) While both skill and vigour can be constrained by energetic demands, skill is also subject to constraints that may arise from biomechanics, muscle architecture and the development of a capacity for

67 coordinated movement (Mancia et al. 2016), which is assumed to be related to neurological
68 development (Byers et al. 2010).

69 In these distinctions between vigour and skill, it seems that there is some overlap
70 between the two concepts as both may be constrained by physiological systems and by
71 energy demands, and both are linked to *temporal* variation in behaviour. However, skill, thus
72 defined, also encompasses an element that is absent in respect of vigour. This is variation in
73 the *spatial* component of expressed behaviour, that is, in the patterns of the movements
74 performed. Therefore, analyses that seek to determine whether skill is functionally significant
75 should focus on analysis of variation in movement patterns. Typically, these movement
76 patterns can be compared between individuals that achieve an outcome and those that fail to
77 achieve an outcome that is dependent upon the behaviour in question.

78 It has already been suggested that the spatial component of motor coordination can
79 yield information on individual quality in other contexts where one individual attempts to
80 convince another to make a decision in the sender's favour. During courtship, females can be
81 attracted to males that display skilfully as well as vigorously (Byers et al. 2010). For instance,
82 in dancing displays, an element of human courtship behaviour, males that perform specific
83 dance moves in a coordinated way are more successful at attracting females than clumsier
84 dancers (Neave, McCarty, Freynik, Caplan, Hönekopp & Fink, 2011). In the leap displays of
85 blue-black grassquits, *Volatinia jacarina*, the male birds perform an elaborate combination of
86 jumps and vocalisations. Success is determined not only by the number of jumps (vigour) but
87 also by the height of jumping (Manica et al. 2016). Although it is difficult to determine what
88 traits constrain jump height it was suggested that the ability to perform well-coordinated
89 motor movements should contribute to jump height, such that it might represent a correlate of
90 skill. Interestingly, leap rate is negatively correlated with leap height. This correlation is
91 unlikely to be driven by the fact that higher jumps take longer to perform because the birds

92 do not jump continuously, leaving pauses between consecutive jumps that are of greater than
93 the time spent aloft. Therefore, this negative correlation represents a potential trade-off
94 between these two components of the display (Manica et al. 2016).

95 Although contests are not necessarily a result of sexual selection (Briffa & Sneddon,
96 2007; 2010; Briffa & Hardy, 2013), agonistic behaviours show clear parallels with sexually
97 selected displays, as both involve decisions (Mowles & Ord, 2012) based on challenging
98 activities (Briffa & Sneddon, 2007). Thus, if skill is an important feature of courtship
99 displays there is also the potential for skill to differ between the winners and losers of
100 contests. In fact, current contest theory implies that skill could be important for two reasons.
101 First, fights might be settled by a process of 'mutual assessment' whereby each opponent
102 provides its rival with information on its RHP (Taylor & Elwood, 2003; Arnott & Elwood,
103 2009; Briffa & Elwood, 2009). Here, the loser only decides to give up when it has determined
104 that it is the weaker individual by assessing its opponent's behaviour, and the performance of
105 challenging motor patterns could yield information on individual quality (Byers et al., 2010).
106 Second, fights might be settled through 'self-assessment' (Taylor & Elwood, 2003; Arnott &
107 Elwood, 2009; Briffa & Elwood, 2009) where giving up decisions are not dependent on
108 information about the opponent's RHP. Here, the loser is the first individual to reach a cost
109 threshold, the maximum limit of costs that an individual is either willing or able to bear.
110 Thus, repeated signals demonstrate stamina and the contest is won by the individual with
111 greater endurance (although in the case of injurious fights, the injuries may also contribute to
112 the accumulation of costs, see Payne 1998; Briffa & Elwood 2009). In this case skill could be
113 important because performing the behaviour efficiently could delay the onset of fatigue.

114 We do not yet know whether skill contributes to the outcome of animal contests in
115 either of these two ways. In contrast, well-coordinated motor patterns are known to influence
116 outcomes in the analogous situation of combat sports in humans. During boxing, for example,

competitors that land their punches on their opponent more accurately are more likely to win (Ashker, 2011). Repeated striking of the opponent also takes place in fights between European hermit crabs, *Pagurus bernhardus*, over the ownership of empty gastropod shells. These serve as 'portable burrows' protecting the crabs from predators and buffering them against variation in the external environment. The opponents take on distinct roles characterised by different behaviours. The smaller of the two crabs usually adopts the role of 'defender', spending the majority of the fight tightly withdrawn into its shell, resisting the attempts of its larger opponent, the 'attacker', to evict it by pulling it out of its shell through the aperture (Fig. 1). In order to secure an eviction, attackers must perform vigorous bouts of shell rapping. Attackers grasp the shell of the defender using their walking legs. Then they use their abdominal musculature to repeatedly move their shell towards and away from the shell of the defender, so that the defender's shell is struck by a rapid succession of raps. Successful attackers perform more raps per bout of rapping, hit harder and often leave shorter pauses between bouts of rapping compared to those that give up without evicting the defender. They also show greater escalation in the rate of rapping compared to attackers that are unsuccessful, and the differences in the vigour of rapping between the two outcomes become more marked towards the end of the fight (Briffa et al., 1998). Analysis of post-fight metabolites indicates that vigorous shell rapping is a challenging behaviour that exceeds the energetic requirements of routine activity (Briffa & Elwood, 2004). Previous analyses have focussed on the vigour of shell rapping (Briffa et al. 1998; Briffa & Elwood 2000a; 2000b; Briffa, Elwood & Russ, 2003) but, as yet, none have addressed the spatial component of the movements used in shell rapping. A simple measure of the spatial component for shell rapping is the distance that the attacker moves its shell away from the defender's shell prior to each strike, which we refer to as 'displacement distance'. Given that shell rapping involves repeated strikes of the attacker's shell against the defender's we expect that there should be

an optimal displacement distance. Displacement distances that are too short might reduce the impact of individual raps but distances that are too long could make rapping inefficient, effectively wasting effort.

If skill contributes to RHP in hermit crabs, there should be variation among attackers in displacement distance, corrected for crab size. These differences in displacement distance should influence the decision of defenders to give up leading to a difference between fight outcomes (evictions and non-evictions). Since shell rapping is a demanding activity (Briffa & Elwood, 2004; Mowles, Cotton & Briffa 2009; 2010) we should see covariation between displacement distance and vigour, either because the two components are traded-off or because efficient movements delay the onset of fatigue. Third, if the spatial component of shell rapping is constrained by energetic state, we should see temporal changes in displacement distance as the fights progress, and winners should be better at maintaining optimal displacement compared to losers. Such relations between displacement distance, vigour and outcomes would indicate that the spatial component of skill influences fight outcomes and hence access to a critical resource.

Materials and methods

Collecting crabs and staging fights

Hermit crabs were collected from Hannafore Point in Looe, Cornwall, UK between February and May 2014. The crabs were kept in groups of 70-100 individuals in 80 litre tanks of aerated seawater at 15°C in a 12h:12h light:dark cycle. They were fed *ad libitum* on white fish. Crabs were removed from their gastropod shells by carefully cracking the shell in a bench vice. Only male crabs that had not recently moulted, and that were free of missing appendages and obvious

parasites were used. All other individuals were provided with a new shell and returned to the sea.

Each crab was weighed and then allocated to a pair consisting of a larger (potential attacker) and smaller (potential defender) crab. The larger crab of each pair was provided with a shell that was 50% of its preferred shell weight. The smaller crab was given a shell that was 100% of the larger crab's preferred shell weight. Preferred shell weights were obtained from regression equations derived from a previous shell selection experiment (Briffa & Elwood 2005). Following provision of the new shell each crab was placed into a 12cm diameter plastic dish containing seawater as above, and allowed to acclimate to the new shell for 15-20 hours. Following this period, fights were staged in an identical plastic container, which was placed behind the one-way mirror of an observation chamber, such that the observer could not be seen by the crabs. The larger crab was placed into the dish first, followed by the smaller crab after a 5-minute interval. Video recordings of each fight were made using a GoPro HERO 3+ camera mounted directly above the container. One hundred and thirty-three contests were staged. Rapping occurred in eighty-three of these, but any fights where the video footage was not of sufficient quality to observe the movements of attackers' shell during rapping were excluded. This left a total of 78 fights for analysis.

The temporal pattern of shell rapping was scored from the video recordings using The Observer XT software. We also recorded the outcome of each fight (eviction or non-eviction). For each rap, individual frames were then extracted from the video recording using KMPlayer software. These frames were then analysed using ImageJ software to find the frame with the maximum displacement distance between the attacker's and defender's shells for each rap. Maximum displacement distance was defined as the shortest distance between the outer margin of the body whorl of the attacker's shell and the parietal wall of the defender's shell, the latter being the point of impact on the ventral shell surface of the defender's shell near the aperture.

Displacement distances were calibrated using the average of two marks of known length (3mm) made on the surface of the attacker's shell, which could be clearly seen in the video recordings. From our record of the temporal pattern of shell rapping we calculated the total number of raps, the number of bouts of rapping, the mean number of raps per bout, and the mean duration of pauses between bouts (Briffa et al. 1998). Bouts were defined as being terminated when the duration between two consecutive raps was >1s (see Briffa and Elwood 2000a for details). Previous studies have indicated that the vigour of shell rapping varies from bout to bout and that over the last four bouts of fighting the pattern of change between bouts differs between successful attackers and those that give up without evicting the defender (Briffa et al. 1998). Therefore, we also calculated the number of raps in each of the last four bouts. For displacement distance, we calculated the mean displacement distance overall for each fight and the mean displacement distance for raps in each of the last four bouts of rapping in each fight.

Statistical methods

Displacement distance unsurprisingly showed a positive correlation with attacker weight ($\log_{10}$ transformed data), whereby large attackers moved their shells further than smaller attackers (Pearson correlation: $r_{76} = 0.32$, $P < 0.005$). There was also a positive correlation with defender weight ($r_{76} = 0.39$, $P < 0.0005$), such that the displacement distance increased as attackers fought larger defenders. In this study we sought to minimise the range of size differences between opponents, such that there was a strong correlation between attacker and defender weight ($r_{76} = 0.95$, $P < 0.0001$). Therefore, it would be inappropriate to include both measures (attacker and defender weight) as covariates in the same analysis. We thus compared displacement distance among successful and unsuccessful attackers using an ANCOVA (where relative weight difference (RWD), which encompasses both attacker and defender weights in

a single variable (Briffa et al., 2013), was included as a covariate. Measures of the vigour of rapping (total raps, total bouts of rapping, mean raps per bout, mean duration of pauses between bouts) were analysed in the same way. All response variables were $\log_{10}$ transformed prior to analysis to improve normality. We used a general linear mixed effects model to determine whether the displacement distance varied across the last four bouts of fighting and whether any pattern of variation differed between outcomes. The response variable was displacement distance and the fixed factors were bout number (4^{th} last to last), outcome, relative weight difference and the interactions between these variables. Fight ID was assigned a random intercept in order to account for repeated measures of the number of raps per bout within each fight. Degrees of freedom were estimated using the Kenward-Roger method, such that *F*-values could be used to infer significance. We also used a similar analysis to investigate changes in the mean number of raps per bout over the last four bouts of rapping. Analyses were performed in the R base package (R Core Team, 2014) and using the lme4 (Bates, Maechler, Bolker & Walker, 2014) and lmerTest (Kuznetsova, Brockhoff & Christensen, 2014).

Ethical Note

Using a bench vice to remove the crab from its shell does not injure the crabs and no crabs were injured during this experiment. At the end of the experiment, all crabs were fed, we ensured that each had a gastropod shell of suitable size and they were all returned to the sea at their point of origin. No licences or permissions are needed to collect hermit crabs and their use in experiments is not covered by any UK legislation.

Results

There was no interaction effect between outcome and RWD on the total number of raps ($F_{1,74}$ = 0.85, P = 0.36), therefore the interaction effect was removed from the model and the ANCOVA was recalculated with main effects only. The number of raps did not vary with RWD

($F_{1,75}$ = 1.28, P = 0.26) but attackers that evicted the defender performed more raps than those that failed to evict the defender ($F_{1,75}$ = 11.59, P = 0.001). There was no interaction effect between outcome and RWD on the total number of bouts ($F_{1,74}$ = 0.77, P = 0.38), therefore the interaction effect was removed from the model and the ANCOVA was recalculated with main effects only. The number of bouts did not vary with RWD ($F_{1,75}$ = 0.76, P = 0.38) but attackers that evicted the defender performed more bouts than those that failed to evict the defender ($F_{1,75}$ = 5.91, P = 0.017). There was no interaction effect between outcome and RWD on the mean number of raps per bout ($F_{1,74}$ = 0.001, P = 0.98), therefore the interaction effect was removed from the model and the ANCOVA was recalculated with main effects only. The number of raps per bout did not vary with RWD ($F_{1,75}$ = <0.001, P = 0.99) but attackers that evicted the defender performed more raps per bout than those that failed to evict the defender ($F_{1,75}$ = 4.69, P = 0.034). There was no interaction effect between outcome and RWD on the mean duration of pauses ($F_{1,64}$ = 0.11, P = 0.75), therefore the interaction effect was removed from the model and the ANCOVA was recalculated with main effects only. The duration of pauses did not vary with RWD ($F_{1,65}$ = 0.59, P = 0.45) and there was no difference in pause duration between outcomes ($F_{1,765}$ = 0.99, P = 0.32). Note that the degrees of freedom for analysis of pauses is lower than for the other parameters because 10 fights only contained one bout and hence had no pauses. There was no interaction effect between outcome and RWD on the displacement distance of the attacker's shell ($F_{1,74}$ = 0.35, P = 0.43), therefore the interaction effect was removed from the model and the ANCOVA was recalculated with main effects only. Displacement distance did not vary with RWD ($F_{1,74}$ = 1.21, P = 0.28) but attackers that failed to evict the defender displaced their shells further than those that evicted the defender ($F_{1,75}$ = 9.21, P = 0.003) (Fig. 2). Both the mean number of raps per bout (Pearson correlation: r_{76} = -0.23, P = 0.04; Fig. 3a) and the total number of raps (Pearson correlation: r_{76} = -0.39, P = 0.0004; Fig. 3b) decreased with increasing displacement distance. All attackers decide to

terminate single bouts of rapping, however the decision to terminate a fight is only made by the subset of attackers that decide to give up. Therefore, we also tested for a correlation between displacement distance and the total number of raps only in fights that ended with a non-eviction. In this subset of fights, that had been terminated by the decision of the attacker, there was also a negative correlation between displacement distance and the total number of raps (r_{21} = -0.56, P = 0.009).

During the last four bouts of rapping there were no overall effects of outcome ($F_{1,212.98}$ = 1.30, P = 0.26), bout number ($F_{1,192.48}$ = 0.05, P = 0.83) or RWD ($F_{1,203.22}$ = 0.06, P = 0.81) on displacement distance, and there was no interaction between bout number and RWD ($F_{1,187.05}$ = 0.1, P = 0.76). However, a significant interaction between outcome and bout number indicates that for successful attackers the displacement distance decreased, whereas for attackers that gave up without evicting the defender the displacement distance increased across the last four bouts ($F_{1,192.48}$ = 8.02, P = 0.005) (Fig. 4). There was also a significant interaction between outcome and RWD whereby displacement distance increased with RWD for unsuccessful attackers but declined with RWD for successful attackers ($F_{1,203.22}$ = 4.26, P = 0.04) (Fig. 5). There was also a significant three-way interaction between outcome, bout number and RWD ($F_{1,187.05}$= 5.56, P = 0.02) indicating that this difference in relationships between RWD and displacement distances between successful and unsuccessful attackers became more marked over successive bouts.

In the analysis of changes in the number of raps per bout over the last 4 bouts, there was no three-way interaction and no interactions between outcome and RWD or bout number and RWD so these effects were deleted and the model recalculated containing only main effects and the interaction between bout number and outcome. There was no main effect of outcome ($F_{1,229.1}$ = 1.07, P = 0.30), bout number ($F_{1,195.58}$ = 0.14, P = 0.71) or RWD ($F_{1,72.48}$ = 0.0002, P = 0.98). However, a significant interaction between bout number and outcome indicates that

for successful attackers the mean number of raps increased across bouts whereas the number of raps declined from bout to bout for attackers that gave up without evicting the defender ($F_{1,195.39} = 8.87$, $P = 0.003$) (Fig. 6).

Discussion

As defined by Byers et al. (2010) the repetitive performance of challenging behaviours can vary in terms of both vigour and skill, and our primary means of detecting variation in skill is to analyse its spatial component, i.e. the movement patterns performed (Manica et al., 2016). In the present study, vigour is quantified by the number of raps per bout (rate of activity) and by the total number of raps (duration of activity), whilst the spatial component of skill is quantified by the displacement distance of the raps. While high vigour is associated with winning a fight it now appears that precise movements are also important. Attackers that failed to evict the defender showed a clear pattern of greater displacement compared to those that were successful.

One possible explanation for the difference in displacement distance between outcomes is that it is driven by the defensive behaviour of successful defenders that resist eviction. Attackers can monitor their own performance (Edmunds & Briffa 2016) and displacement distance might correlate with the power supplied to each rap. Greater displacement therefore might represent a strategy that attackers use in an attempt to overcome especially stubborn defenders. We did not assess the power of shell rapping in this study but this explanation seems unlikely. Assuming that the fighting ability of defenders relative to attackers increases as their sizes become more similar (Briffa et al. 1998), then if greater displacement represents a strategy for dealing with high quality defenders we would expect to see a negative relation between RWD and displacement distance (i.e. as attackers get larger

relative to defenders they would be displacing their shells by shorter distances). Across the whole fight these was no correlation between displacement distance and RWD. During the last 4 bouts where this effect might be expected to be most apparent we did find correlations between RWD and displacement. However, for those attackers that failed to evict the defender displacement increased slightly with RWD such that they displaced further against relatively weaker defenders.

Whilst facultative increases in displacement in response to the fighting ability of defenders seem unlikely, the differences in this spatial component of shell rapping between outcomes are consistent with the idea that successful and unsuccessful attackers differ in the ability to perform well-coordinated motor movements, that is they differ in skill. Although skill and vigour can be distinguished through the definitions suggested by Byers et al. (2010) disentangling the relative contribution of these two components may be less straightforward (2010) both in the present study and in other examples. In the present example, both aspects contribute to positive outcomes for attackers. Indeed, individuals that performed more raps also showed low displacement, so it appears that skill and vigour co-vary, similar to courtship displays in *V. jacarina* (Manica et al., 2016).

There are two potential explanations for the association between displacement distance and the vigour of shell rapping. First, they could be relatively independent traits, and individuals of high underlying quality can rap skilfully (maintaining short displacement distances) as well as vigorously. Although skill has been understudied in the context of agonistic behaviour there are several examples of enhanced expression across a suite of signalling traits in high quality individuals. For example, in the sexually selected displays of male fiddler crabs, *Uca tangerii*, males wave their major cheliped and roll mud balls from the sediment that they excavate from their burrows. Males that wave their claws at a greater rate also make mud balls more efficiently and females choose males on the basis of both

behaviours (Latruffe, McGregor& Oliveira, 1999). A difference between this example and the current one is that in the fiddler crabs there are two distinct behaviours involved in the sexual displays whereas here we focus on two components of the same behaviour. A second explanation is therefore that vigour and displacement distance are functionally linked such that rapping vigorously is dependent upon forming the motor movements skilfully. Shorter displacement distances, for example, could allow smaller intervals between successive raps and hence a greater rate of rapping within each bout, which is known to influence the chance of an eviction (Briffa & Elwood 2000a). Here, we found that attackers that displaced their shells further performed fewer raps per bout and fewer raps in total, the latter result still being present when only those attackers that decided to give up were included in the analysis. Thus, attackers that rap with high displacement also decide to terminate both individual bouts of rapping and entire fights sooner than those that rap with lower displacement. These differences, in the number of raps per bout and persistence in a fight, have been shown to be driven by accumulated energetic costs (Briffa & Elwood 2004). Therefore, rather than skill and vigour components being traded off against one another as seen for displays in *V. jacarina* (Manica et al. 2016), we suggest a different explanation for the covariation between the vigour and skill of shell rapping in *P. berhnardus*; lower displacement might allow for less energy expenditure per rap. In this case more raps could be performed delaying the onset of fatigue in attackers and thus allowing them a greater chance of persisting until the defender crosses its own threshold (Briffa & Elwood 2004) for giving up. Conversely, those attackers that perform the movements less well (by displacing their shell further than is necessary) might be wasting effort, such that they can perform fewer raps before giving up. If skill and vigour are functionally linked they should not be regarded as independent RHP traits. Rather, performing the movements involved in shell rapping skilfully could be necessary for the sustained vigorous rapping that is associated with evictions. These scenarios have parallels

362 with those suggested for the evolution of social competence (Taborsky & Olivera, 2012). In
363 social settings, including contests, competence in interactions with other individuals may
364 evolve independently across a range of different behaviours, or the expression of social
365 behaviours may show positive covariation. These explanations (independent traits or
366 functionally linked traits) for the link between skill and vigour are not mutually exclusive.
367 Indeed, both are compatible with our result that skill differs between fight outcomes.

368 In addition to defining skill as performing a challenging activity well, Byers et al.
369 (2010) also suggest that for skill to be an adaptive component of animal signalling it should
370 be assessed by receivers. In the case of shell rapping lower displacement distances by
371 attackers are indeed associated with giving up decisions in the defenders that receive shell
372 rapping. Previous studies have shown that defenders that receive vigorous rapping are more
373 likely to give up and our assumption has therefore been that vigour is the key feature that
374 defenders assess (Briffa & Elwood, 2004; Mowles et al., 2009; 2010). Furthermore, vigorous
375 shell rapping appears to inflict direct physiological costs on defenders (as well as on the
376 attackers that perform the raps) (Briffa & Elwood, 2004; 2005), potentially because the
377 resulting vibrations of the defender's abdominal muscles cause a reflex stiffening (Chapple,
378 1993). Nevertheless, defenders still appear to assess the pattern of rapping because those that
379 receive vigorous rapping at the start of the fight give up sooner compared with defenders that
380 are eventually evicted but receive weak rapping at the start of the fight (Briffa & Elwood
381 2002). In contrast, it is improbable that defenders could visually assess the movement
382 patterns performed by attackers directly, because they spend the shell rapping phase of the
383 fight withdrawn into their shell and would be unable to observe the movements of attackers.
384 Rather, defenders might assess the sustained vigour that short displacement distances allow,
385 rather than the displacement distances *per se*. Nevertheless, if attackers that rap skilfully,
386 avoiding wasteful effort on larger displacement distances, are better able to sustain vigorous

rapping then skilful rapping should still be adaptive even if skill is not directly assessed by defenders. This is perhaps a key difference between the tactile behaviours analysed here and the visual and acoustic displays discussed by Byers et al. (2010) and recently analysed in birds (Manica et al. 2016), where receivers can directly observe (and hear) all aspects of a display.

If displacing the shell too far reduces the chance of evicting the defender, why would some attackers do this? One suggestion for variation in skill is that it reflects underlying differences in individual quality, driven by variation in genes, condition and development, which ultimately drive variation in the neuronal and muscular machinery required for coordinated movement (i.e. motor control) (Byers et al. 2010). In addition, skill might be honed as a result of accumulated experiences. For example, in many species individuals with experience of winning a fight are more likely to win subsequent fights (Hsu, 2001; Hsu & Wolf 1999; Hsu, Earley & Wolf, 2006). The benefits of experience can even accrue across different contexts. In the hermit crab *P. nigrofascia* prior experience of copulation increases the chance of success in subsequent agonistic encounters (Yasuda, Matsuo, & Wada, 2015). Assuming that larger hermit crabs are older (Lancaster, 1998) and hence more experienced, we found limited evidence that experience might influence skill. In fights where there was an eviction, the displacement distance decreased as the size of attackers relative to defenders increased. In contrast, for attackers that failed to evict the defender, displacement distance increased with increasing relative size of attackers. However, when we compared displacement distance against the absolute size of attackers we found a positive trend, which was most likely driven by larger body sizes constraining the crabs to move their abdomens through greater distances. Thus, it may be difficult to determine the effect of experience on displacement distance by using body size as a proxy for experience.

411 Another possibility is that attackers might vary in their ability to assess the
412 effectiveness of their own shell rapping during a fight. A recent study (Edmonds & Briffa,
413 2016) has shown that attackers assess the effects of their own raps on the defender and if
414 rapping is ineffective they perform a greater frequency of an alternative behaviour, shell
415 rocking. Perhaps then attackers that use short displacement distances are better able to judge
416 the effectiveness of their shell rapping, adjusting the distance towards an optimal
417 displacement as the fight proceeds. Indeed, we found differences in the temporal pattern of
418 variation in displacement distances, between successful and unsuccessful attackers. The
419 behaviour of attackers during the final bouts of the fight is critical to their chances of success.
420 Previous studies (Briffa et al. 1998) and the current data show that successful attackers
421 escalate the vigour of rapping (number of raps per bout) whereas those that give up de-
422 escalate. Here, we show that for successful attackers the displacement distances decrease
423 during the final four bouts, suggesting adjustments towards smaller displacement distances.
424 However, in unsuccessful attackers, we saw the opposite (and stronger) pattern of an increase
425 in displacement across the final four bouts of rapping in those attackers that failed to evict the
426 defender. In terms of effective shell rapping, this trend mirrors the differences between
427 successful and unsuccessful attackers in terms of vigour during the same critical period of the
428 fight. The decline in vigour is linked to accumulated energetic costs of shell rapping in
429 attackers, such as the accumulation of muscular lactate, and theory predicts de-escalation in
430 the rate of agonistic behaviour as a result of fatigue (Payne & Pagel, 1997). Therefore, the
431 increase in displacement in unsuccessful attackers might also be a related to fatigue.
432 Although the links between fighting skill and fatigue have been understudied in animals, they
433 have been analysed to an extent in the context of combat sports in humans. In a study of
434 three-bout boxing contests, offensive skill was defined as the proportion of punches that
435 landed on target (Ashker, 2011). For both winners and losers, the proportion of on-target

436 punches declined across the three bouts of intensive combat (Ashker, 2011). Furthermore, the
437 vigour of punching (number of punches per bout) was maintained across all three bouts for
438 winners but declined for losers (Ashker, 2011). Thus, there are striking similarities between
439 the shell rapping behaviour of attacking hermit crabs and the punching behaviour of human
440 boxers. In both examples it appears that skill (displacement distance in hermit crabs and on-
441 target punches in boxers) declines with contest duration, such that the accuracy (as well as the
442 vigour) of agonistic behaviour is reduced by fatigue. If displacement distance indicates
443 wasteful effort, it appears that the amount of effort wasted increases with fatigue levels,
444 perhaps due to a loss of coordination in the required motor patterns. The fact that skill levels
445 can both increase and decrease in fights is relevant to the question of how fighting animals
446 make their decisions to give up. If skill is subject to the effects of fatigue, the presence of
447 both patterns (as seen in the current data) lends support to the idea that giving up is based on
448 self-assessment, as models based on this assumption are the only ones compatible with
449 escalation and de-escalation of agonistic behaviour (Payne & Pagel 1997; Payne 1998); in
450 contrast, mutual assessment models predict that agonistic behaviour should be performed
451 consistently within phases of a fight (Enquist & Leimar 1983).

452 Both vigour and the spatial component of movement patterns involved in shell
453 rapping are important determinants of contest outcomes in hermit crabs. According to the
454 definitions of skill given by Byers et al. (2010) the accuracy of the movement patterns
455 involved in shell rapping reflects the skill of attackers, i.e. their ability to perform a
456 demanding activity well. Nevertheless, our data also indicate that skill and vigour are
457 interlinked, and that both may vary as a result of fatigue. Performing with sustained vigour
458 may be dependent upon the ability to skilfully perform the movements involved. Individuals
459 that waste effort by displacing their shells too far perform fewer raps and are less likely to
460 win the fight. Therefore, we suggest that in the context of animal contests, movement patterns

do not need to be directly observed or assessed by opponents for skill to be an important determinant of fight outcomes. There are many other examples of agonistic displays based on repetitive movement patterns where skill as well as vigour might be an important correlate of RHP, and further studies into the role of skill during fights could provide new insights into strategic decision-making during animal contests. In particular, there is the potential for a greater understanding of how individuals use prior experiences and information gathering within fights to hone their fighting skill, and how these abilities interact with the costs of fighting, which appear critical to the chance of winning.

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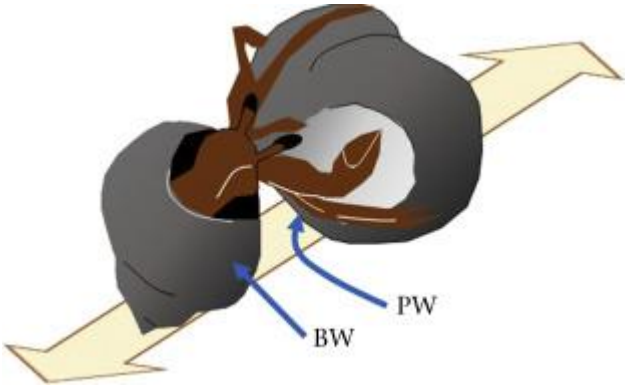


Figure 1: Diagrammatic illustration of two hermit crabs engaged in a shell fight. The attacker is on the left and the defender is on the right. The defender's chelipeds would normally be visible in the aperture of its shell but these are omitted for clarity (the attacker's antennae and antennules are also omitted). During shell rapping the attacker strikes the body whorl (BW) of its shell against the defender's shell adjacent to the parietal wall (PW) of the defender's shell. To effect these strikes, the attacker moves its shell back and forth in the plane indicated by arrows.

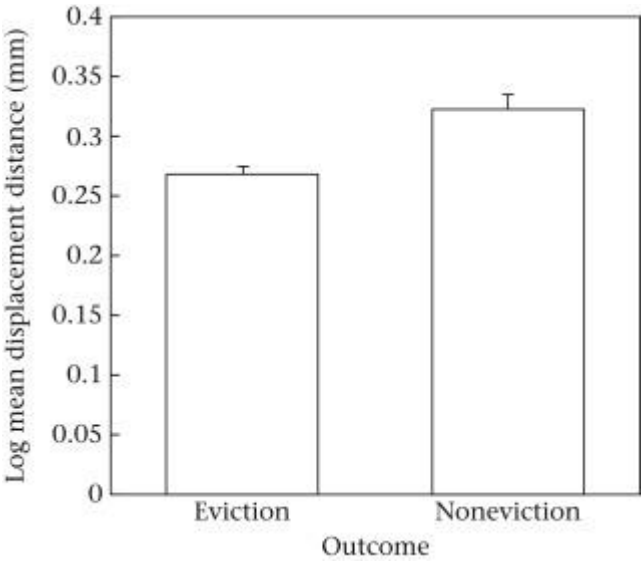


Figure 2: The difference in the mean displacement distance of shell rapping performed by attackers between fights that ended in evictions and non-evictions. Error bars show standard errors.

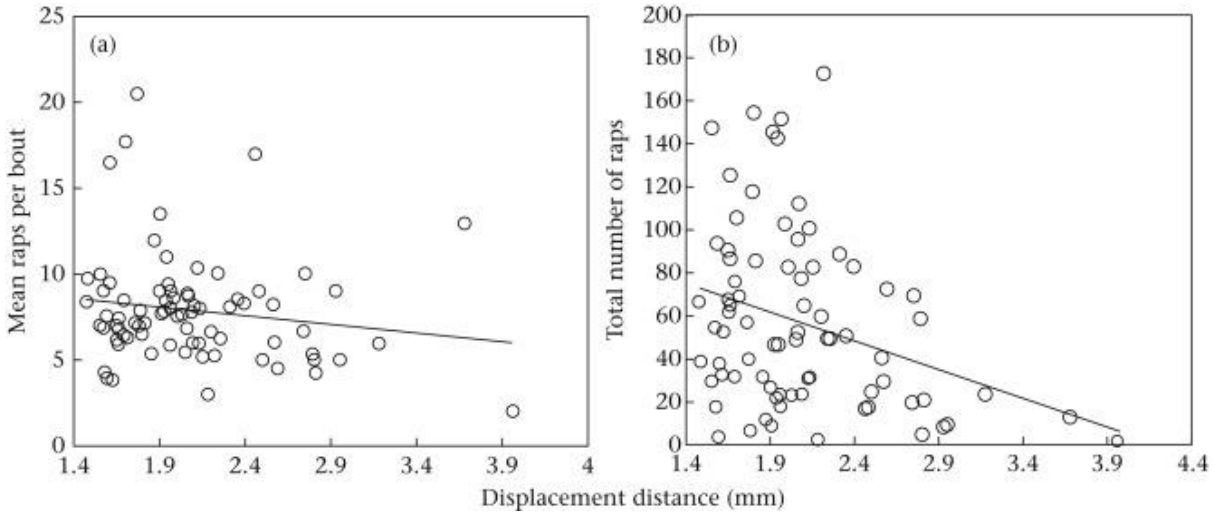
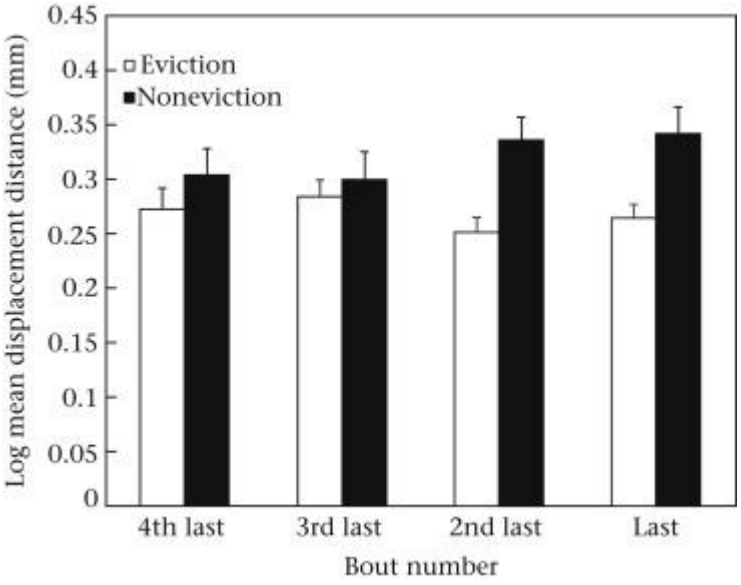


Figure 3: The significant negative correlations between displacement distance and (a) the mean number of raps per bout and (b) the total number of raps performed by attackers. Regression lines fitted for illustration.



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611 **Figure 4:** The change in mean displacement distance across the last four bouts of rapping, for

612 fights that ended in evictions and non-evictions. Error bars show standard errors.

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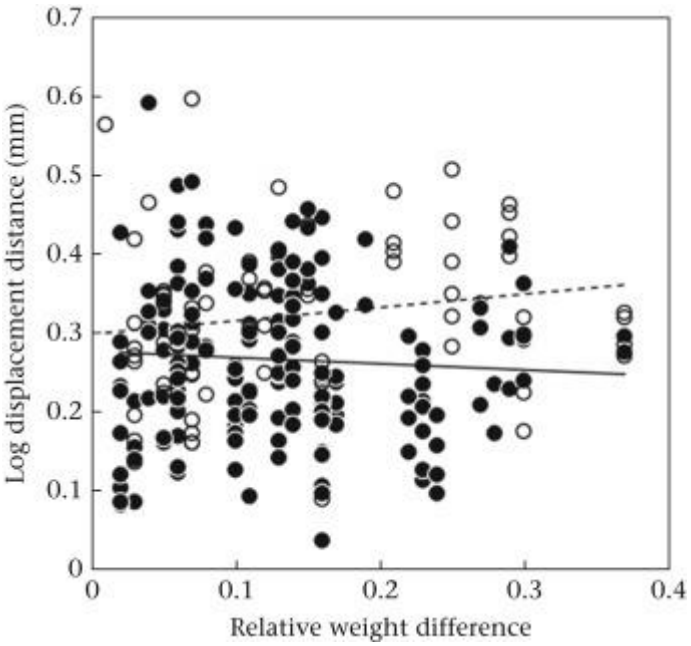

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615 **Figure 5:** The correlation between relative weight difference (RWD) and displacement

616 distance for fights that ended in an eviction (solid circles, solid line) and non-evictions (open

circles, dashed line), for raps performed during the last four bouts. Regression lines fitted for illustration.

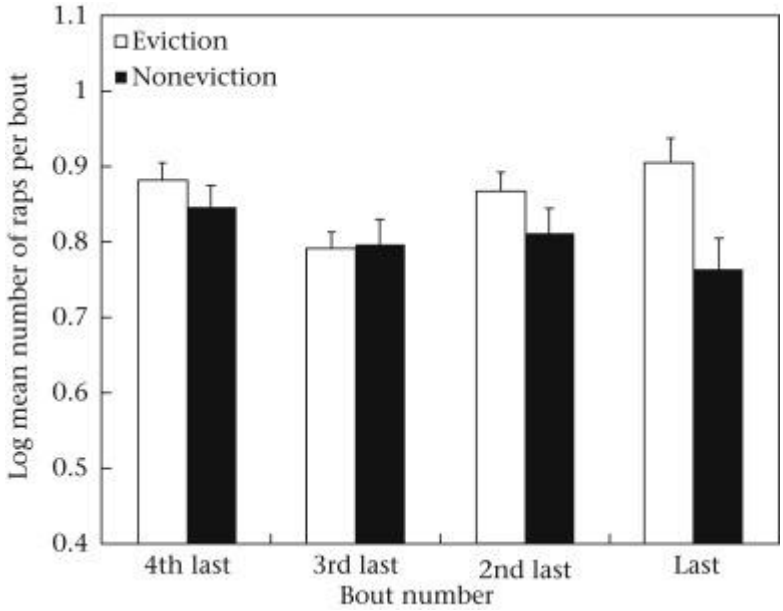

Figure 6: The change in the mean number of raps per bout across the last four bouts of rapping, for fights that ended in evictions and non-evictions. Error bars show standard errors.

Highlights

- Fight behaviour varies in vigour fighting skill has yet to be analysed
- Skill describes the precision of coordinated movement
- Victorious hermit crabs displaced their shells by less distance than losers
- Displacement distance varied with vigour and as fights progressed
- Skill as well as vigour contributes to fighting ability in hermit crabs